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Comparison of Feeding Behavior between Two Different-Sized Groups of Japanese Macaques (*Macaca fuscata yakui*)

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Short title: Feeding competition in Japanese macaques

13 **ABSTRACT**

14 Group-living animals face intragroup scramble and intergroup contest competitions.
15 Many studies have shown that larger groups bear the costs of intragroup scramble
16 competition, which negatively affects the reproductive success of females. Unlike most
17 primate species, Japanese macaques in the Yakushima coastal forest show increased
18 reproductive success with group size. However, it remains unclear how group size
19 affects the behavior of macaques. The present study examined the effects of group size
20 on the feeding behavior of Japanese macaques in the Yakushima coastal forest. We
21 investigated 9–13 adult females from two different-sized groups via focal animal
22 sampling during October 2012–August 2013. We compared the feeding behavior,
23 including patch use, between the two groups. The larger group had a larger home range
24 and spent more time feeding, especially on mature leaves. This suggests that intragroup
25 feeding competition should be more intense in the larger group than in the smaller group.
26 The feeding of mature leaves might enable the larger group to increase the number of
27 co-feeding individuals. Contrary to the predictions that the larger group travels longer
28 distances and spends more time moving, the smaller group traveled longer distances and
29 spent more time moving, although the number of visited patches did not differ between
30 the two groups. The immediate consequences of the loss of intergroup encounters could
31 accumulate as daily travel costs, considering that group size is associated with
32 intergroup dominance and that intergroup aggressive encounters occur frequently in the
33 Yakushima coastal forest. This suggests that the smaller group has increased travel costs
34 as a result of intergroup contest competition, which leads to decline in reproductive
35 success.

36 Key words: feeding competition; ecological constraints model; patch use; group size;
37 *Macaca fuscata yakui*

INTRODUCTION

Group living has benefits such as resource defense (advantage in intergroup feeding competition) [Wrangham, 1980], predator avoidance [Hamilton, 1971], and efficient resource detection [Struhsaker, 1981], and includes costs such as intragroup feeding competition [Janson & van Schaik, 1988] and disease transmission [Sanderson et al., 2014]. Feeding competition has been considered the most important factor affecting the fitness of group-living animals [Chapman et al., 2012]. Animals in groups face two types of group-size-dependent feeding competition: intragroup scramble competition and intergroup contest competition.

Intragroup scramble competition occurs when animals use the same food patches, thereby reducing the amount of food intake per capita for all members of the group [Janson & van Schaik, 1988; Koenig, 2002]. Its intensity increases with group size because larger groups need more food resources. The ecological constraints model [Chapman & Chapman, 2000] predicts that the larger groups are required to visit more food patches, which forces them to have larger home ranges, to travel longer distances and to spend more time feeding and moving. Two mechanisms are assumed to explain the need for more patches. One is patch depletion: a larger number of animals leads to faster depletion of food resources [Chapman & Chapman, 2000]. The other is spatial compression (termed “funneling”): larger groups will fill in a food patch more quickly because the patch can accommodate a limited number of animals. Therefore, animals in larger groups will leave the patch earlier and move further to the next patch than those in smaller groups because they will be pushed forward by succeeding animals [Isbell, 2012].

The costs of intragroup scramble competition could influence the fitness of group-living animals [Koenig, 2002]. Most of the studies have demonstrated

disadvantages of larger groups: the costs of intragroup scramble competition negatively affect the net energy gain / reproductive success [van Schaik et al., 1983; van Noordwijk & van Schaik, 1999; Borries et al., 2008; Zhao et al., 2011]. Meta-analysis on the relationship between group size and behavior and demography [Majolo et al., 2008] also support the predictions of the ecological constraints model. This study concludes that, in most primate species, the costs of intragroup feeding competition balanced or outweighed the benefits of intergroup feeding competition which lead to higher net energy gain / reproductive success in large-sized, dominant groups than in small-sized, subordinate groups through intergroup encounters [Janson & van Schaik, 1988; Koenig, 2002]. However, several studies have revealed different patterns of relationships between net energy gain / reproductive success and group size [Cheney & Seyfarth, 1987; Robinson, 1988; Koenig, 2000; Takahata et al., 2006]. In particular, it remains untested the predictions of the ecological constraints model and unclear how group size affects behavior when the net energy gain / reproductive success increases with group size.

Among Japanese macaques (*Macaca fuscata yakui*) of the Yakushima coastal forest, larger groups have higher birth rates than smaller groups [Suzuki et al., 1998; Takahata et al., 1998]. Since group density is high (4.8 groups/km^2) [Yoshihiro et al., 1999] and the home range is worth defending against other groups [Maruhashi et al., 1998], aggressive intergroup encounters occur frequently [Saito et al., 1998; Sugiura et al., 2000; Hanya et al., 2008]. The outcome of intergroup encounter is determined by the relative group size: larger groups are dominant over smaller groups [Sugiura et al., 2000]. Based on these results, previous studies have suggested that larger groups, which have advantages in intergroup encounters, achieve higher reproductive success [Suzuki et al., 1998; Takahata et al., 1998]. Japanese macaques in the Yakushima coastal forest

are ideal subjects to investigate the relationships between group size and feeding competition because the effects of predation pressure on group size can be ignored owing to the absence of predators in this region [Yamagiwa & Hill, 1998]. Majolo et al. [2009] clarified that a larger group had a larger home range, traveled longer distances, and spent more time moving than did a smaller group. These results supported the predictions of the ecological constraints model, and showed that intragroup scramble competition was more intense in the larger group. However, more detailed study is needed to elucidate the mechanisms whereby, in contrast to most primate species, reproductive success declines as group size decreases. It is necessary to investigate feeding behavior thoroughly, including food patch use, which is the assumption of the ecological constraints model. This investigation should be conducted under controlling habitat quality, to avoid obscuring the effects of group size on feeding behavior [Majolo et al., 2009].

The objective of this study was to reveal effects of group size on feeding behavior including food patch use of Japanese macaques in the Yakushima coastal forest. We compared behavioral proxies of intragroup scramble competition such as home range size, travel distance, activity budget, and the number of visited patches between two different-sized groups. Following the ecological constraints model, we predicted that the larger group will have a larger home range, travel longer distances, spend more time feeding and moving, and visit more patches than the smaller group. Additionally, dietary composition and diversity were compared between the two groups. We predict that the animals in the larger group will consume less-preferred and/or lower-quality foods and increase dietary diversity due to intense intragroup scramble competition [Steenbeek & van Schaik, 2001; Gogarten et al., 2014]. We also compared four characteristics of patch use: patch residency time, patch size, the number of co-feeding

113 individuals, and inter-patch distance. According to the ecological constraints model, we
114 predicted that patch residency time will be shorter and the number of co-feeding
115 individuals will be larger in the larger group than in the smaller group. Patch size and
116 inter-patch distance will not differ between the two groups due to the similarity of
117 habitat environment. In addition, we examined two assumptions underlying the
118 ecological constraints model. First, to examine patch depletion, we compared feeding
119 rate between the two groups and examined the relationship between feeding rate and
120 patch residency time. If the patch depletion occurs more frequently in the larger group,
121 feeding rate in the larger group is expected to be lower than that in the smaller group,
122 which leads to shorter patch residency time. Second, to examine funneling, we
123 compared proportions of patches within which the maximum number of animals
124 outweighs the number of feeding sites between the two groups, and tested whether
125 patch residency time was shortened in such patches. If funneling occurs more frequently
126 in the larger group, animals in the group fill in feeding sites in the patch more frequently,
127 which leads to shorter patch residency time.
128
129 **METHODS**
130 This study was conducted with permission from the Yakushima Forest Ecosystem
131 Conservation Center and Kagoshima Prefectural Government, complied with the ethical
132 guidelines for field research of non-human primates of the Kyoto University Primate
133 Research Institute and the legal requirements of Japan, and adhered to the American
134 Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.
135
136 **Study Site and Groups**
137 We studied two groups (KwA and KwCE, hereafter referred to as larger and smaller

groups, respectively) of Japanese macaques living in the western coastal forest on Yakushima Island (30°N, 130°E) during October 2012–April 2013.The study period included mating season (mid-August–January) [Yamagiwa, 1985]. The study area was covered with primary and secondary warm temperate evergreen broad-leaved forest, mainly comprising Fagaceae, Hamamelidaceae, Myrsinaceae, and Lauraceae [Agetsuma, 1995; Tsujino et al., 2007]. Vegetation was essentially the same in the respective home ranges of each of the two groups because they had partly overlapped home ranges in similar altitudinal zones (ca. 0–350 m a.s.l.). The larger group had 30–35 individuals, including 6–8 adult females (>6 yrs old), 3–6 adult males (>6 yrs old), 15–21 juveniles (1–5 yrs old), and 1–6 infants (<1 yr old). The smaller group had 13–15 individuals, including 4–5 adult females, 4–5 adult males, 2–5 juveniles, and 0–4 infants. The sizes of the larger and smaller groups were larger and smaller than the mean group size of this local population (16.9 individuals) [Yoshihiro et al., 1999], respectively. Neither group exhibited sub-grouping ranging during the study period [Kurihara, unpublished data]. We confirmed that the larger group had advantages in intergroup encounters in accordance with the previous study [Sugiura et al., 2000]: the larger group won two of the four encounters, and the smaller group did not win any encounter (0/8) (larger group: 0.020 times/h; smaller group: 0.067 times/h).

Behavioral Data Collection

We followed one or both of the two groups each day and changed the focal group at least once every three days. We investigated all adult females in the two groups (9–13 individuals) via one-hour focal animal sampling. We changed the focal animal every hour and selected the following one for which the observation time accumulated so far was shortest. Total observation time was 333 h (larger group: 199 h, smaller group: 134

h). Via instantaneous recording, we recorded activities (feeding, moving, resting, grooming and other) of the focal animal every minute. When the focal animal was feeding, we recorded the onset and the end of feeding to the nearest second and feeding items (species and part). We regarded the onset as the time when the focal animal puts food into the mouth, and the end as the time when 20 seconds had passed without manipulating the food. In addition, we recorded feeding rate: the number of food units that the focal animal puts into the mouth per 10 seconds. A food unit was defined for each feeding item (one fruit, one leaf, one cluster of fruits, etc.). The recording was repeated as many times as possible while the focal animal was feeding. We defined a food patch as one individual tree or liana in which the focal animal fed. In the present study, terrestrial patches (fallen fruits / seeds or insects) could not be defined because these foods were uniformly distributed on the ground. When the focal animal left a patch and returned back without feeding in any other patches, we considered it as one patch. If the focal animal fed in a patch, we also collected the following data: (1) time when the focal animal entered into and departed from the patch, (2) time when other individuals entered into and departed from the same patch in which the focal animal fed, and (3) length of major and minor axes and height of the patch. By using GPS (GARMIN 60CSx, GARMIN), we recorded locations of the focal animal every 30 seconds and food patches when the focal animal visited.

Data Analysis

Home Range and Travel Distance

We estimated home range size and calculated travel distance based on GPS data points plotted every five minutes. Home range size was estimated by using fixed kernel density method. The grid size was 10 m × 10 m, and the smoothing parameter h was

188 determined by an *ad hoc* technique because the calculation by the least square cross
189 validation method did not converge. We regarded 95% kernel area as overall home
190 range, and 50% kernel area as the core area. Travel distance was calculated as the sum
191 of linear distance among GPS points plotted consecutively.
192
193 *Diet*
194 Feeding items were categorized into eight types: fruits / seeds, mature leaves, young
195 leaves (including buds and shoots), flowers (including nectar and flower buds), animal
196 matter, fungi, other (pith, bark, water, soil, etc.), and unidentified. Furthermore,
197 fruits/seeds were categorized as fallen (focal animals fed on the ground) or not (on the
198 trees). In addition, foraging (searching for food such as fallen fruits / seeds or insects in
199 the litter on forest floor) was considered as a type of feeding as per Hill [1997]. The
200 feeding behaviors could not be categorized into one specific feeding item, because
201 discriminating whether macaques searched fallen fruits / seeds, insects, or other
202 items in the litter could not be determined, and the food-searching behavior did not
203 always result in actual feeding.
204 To evaluate the monthly diversity of food repertoire, we calculated the
205 Shannon-Wiener index *H*:
206 $$H = -\sum_i pi \ln pi$$
207 where, p_i is the proportion of time spent feeding on the item *i* among the total feeding
208 time. *H* increases with the diversity of food repertoire, and equals zero when one
209 specific feeding item accounts for 100% of the total feeding time.
210
211 *Comparison of Behavioral Proxies of Intragroup Scramble Competition*
212 We constructed generalized linear mixed models (GLMMs) to explain diet composition,

activity budget, travel distance, and the number of visited patches (Table I). The distribution of travel distances was normalized by square root transformation. In the diet composition model, group (larger or smaller) was included as fixed effect and observation date as random effect. To explain feeding on young leaves, we used generalized linear model (GLM) because GLMM did not converge. In the remaining models, group, copulatory behavior and dietary composition were included as fixed effect, and observation date or identities of the focal animals as random effect. It has already been established that diet composition and copulatory behavior affect the overall feeding patterns of animals [Agetsuma, 1995; Matsubara & Sprague, 2004]. The proportions of time spent feeding on fruits / seeds and animal matter were included as factors of diet composition, because seasonal variation in diet could be considered on the basis of these two types of foods. The proportion of time spent feeding on mature leaves, young leaves, flowers, and time spent foraging were correlated with that on fruits / seeds (Spearman's rank order correlation: mature leaves: $\rho = -0.71$, $p < 0.001$; young leaves: $\rho = -0.42$, $p < 0.001$; flowers: $\rho = -0.39$, $p < 0.001$; foraging: $\rho = -0.46$, $p < 0.001$), and the proportion of time spent feeding on fungi were correlated with that on animal matter (fungi: $\rho = 0.56$, $p < 0.001$). As a factor of copulatory behavior, whether male-female mounting series involving the focal animal was observed (1) or not (0) during a one-hour session was included in the models on travel distance and the number of visited patches, and number of one-hour sessions during which the mounting series was observed in a day was included in the model for activity budget.

To examine the effects of "group" on each dependent variable, we compared the models with and without the factor "group" using ANOVA (likelihood ratio test). If $P < 0.05$ was obtained, "group" was regarded as a factor significantly affecting the goodness-of-fit of the models. To examine the difference in the diversity of food

repertoire, the Shannon-Wiener index H of the two groups was compared using Wilcoxon rank-sum test.

Patch Use

To investigate how group size affected the general characteristics of patch use, we compared patch residency time, patch size, number of co-feeding individuals, and inter-patch distance between the two groups. Patch residency time was calculated as the feeding time of the focal animal in a patch to the nearest seconds. When entrance or departure time into / from the patch by the focal animal could not be recorded, the data on patch residency time for the patch was discarded. Patch size was calculated as the volume of an elliptic cylinder (major axis*minor axis*height*π) [Kazahari & Agetsuma, 2010]. The number of co-feeding individuals was calculated as the average number of other individuals (except infants) within the same patch during the focal animal's residency [Hanya, 2009]. If, during a stay for two minutes, three individuals stayed with the focal animal for the first 90 seconds and two individuals for the last 30 seconds, the number of co-feeding individuals in the patch was regarded as 2.75. Inter-patch distance was calculated as linear distance between patches that the focal animal visited consecutively. We constructed GLMMs to explain patch residency time, patch size, and number of co-feeding individuals (Table I). The distributions of patch residency time and patch size were normalized by log transformation. The number of co-feeding individuals was rounded up and transformed to integers to treat as Zero-inflated Poisson distribution. In the model for patch residency time, group, patch size, number of co-feeding individuals, and food category (fruits / seeds, mature leaves, young leaves, and other) were included as fixed effect, and the identities of the focal animal as random effect. In the model for patch size, group and food category were included as fixed

effect, and the identities of the focal animal as random effect. In the model for number of co-feeding individuals, group, patch size, and food category were included as fixed effect, and the identities of the focal animal as random effect. It has already been established that (1) patch residency time is influenced by patch size and number of co-feeding individuals, (2) number of co-feeding individuals is influenced by patch size, and (3) the three characteristics of patch use are influenced by food category [Kazahari & Agetsuma, 2008; Hanya, 2009; Potts et al., 2011]. Likelihood ratio tests were conducted to examine the effects of group on patch residency time and patch size. For the effects of group on number of co-feeding individuals, we examined the significance of "group" in the model because the likelihood ratio test could not be conducted. In addition, inter-patch distance was compared between the two groups using Wilcoxon rank-sum test.

To test whether patch depletion occurred more frequently in the larger group, we compared feeding rate between the two groups and examined correlation between feeding rate and patch residency time. This analysis was conducted for each feeding item separately to minimize effects of patch characteristics [Kazahari et al., 2013]. We selected 12 main feeding items that accounted for 56% (290/516) of all visited patches in the larger group and 43% (163/380) in the smaller group. Feeding rate was averaged for each patch, and compared using Wilcoxon rank-sum test. The correlation between feeding rate and patch residency time was tested using Spearman's rank order correlation. Ideally, we should have examined time-series variations in feeding rate in the patch [Kazahari & Agetsuma, 2008], but it was difficult to collect sufficient data for conducting such an analysis. Although this comparison may be preliminary, group differences in feeding rate could be detected sufficiently.

We tested whether funneling effect shortened patch residency time more

frequently in the larger group. First, we examined the relationships between the maximum number of animals and the number of feeding sites in a patch. The number of feeding sites was calculated by dividing the patch size by 4.18 m^3 (the volume of a sphere with a radius of 1 m, a monopolizable area for one individual) [Hanya, 2009]. We defined a *filled patch* as when the maximum number of animals outweighed the number of feeding sites in the patch. The proportion of the filled patches among all visited patches was compared between the two groups by Fisher's exact test. Second, we examined whether patch residency time was shortened at the filled patches. We constructed GLMM on patch residency time for each group (Table I). The distribution of patch residency time was normalized by log transformation. Whether the patch was filled or not, food category (fruits / seeds, mature leaves, young leaves, and other), and dominance rank of the focal animal were included as fixed effect, the identities of the focal animal as random effect, and patch size as offset term. Dominance rank was determined by the normalized David's scores calculated on the basis of aggressive interaction [de Vries et al., 2006]. A likelihood ratio test was conducted to examine effects of filling patches on patch residency time.

We used the *adehabitat* package for estimating home range and the *lme4* and *glmmADMB* package for GLMM in R 3.0.1.We calculated travel distance and inter-patch distance and visualized the home ranges by QGIS 2.0.1.All statistical tests, except the likelihood ratio test, were two-tailed, and alpha level was set at < 0.05.

RESULTS

Comparison of Behavioral Proxies of Intragroup Scramble Competition

The larger group had a larger home range (Figure 1, larger group: 38.9 ha, smaller group: 34.8 ha) and spent more time feeding than did the smaller group (Tables II, III),

313 although the two groups had the same core areas in size (9.4 ha).

314 Dietary composition was different but dietary diversity did not differ between
315 the two groups. The larger group spent less time feeding on fruits / seeds and young
316 leaves and more time feeding on mature leaves and foraging than did the smaller group
317 (Tables II, III). In particular, fallen fruits / seeds feeding time accounted for a larger
318 proportion of the total fruits / seeds feeding time in the larger group than in the smaller
319 group (Table III, larger group: 29.1% ± 36.2%; smaller group: 15.7% ± 28.5%;
320 likelihood ratio test: $df = 1$, $\chi^2 = 59.18$, $p < 0.001$). There were no differences in feeding
321 time on flowers, animal matter, and fungi (Tables II, III). Further, the monthly diversity
322 of food repertoire did not differ between the two groups (H: larger group: 2.43 ± 0.23,
323 smaller group: 2.40 ± 0.42; Wilcoxon rank-sum test: $W = 18$, $p = 0.58$). Over the study
324 period, 33 species and 57 items were common among the two groups (Appendix I,
325 larger group: 45 species, 83 items; smaller group: 47 species, 84 items). In a month, the
326 common repertoire accounted for 61.7% ± 11.7% of species and 56.7% ± 10.8% of
327 items in the larger group, and 66.7% ± 11.6% and 63.6% ± 12.6% in the smaller group,
328 respectively.

329 Contrary to the predictions, the smaller group spent more time moving (Tables
330 II, III) and traveled longer distances than did the larger group (Table III, larger group:
331 188 ± 72 m/h, smaller group: 219 ± 116 m/h; likelihood ratio test: $df = 1$, $\chi^2 = 7.67$,
332 $p < 0.01$). In addition, there were no differences in the number of visited patches (Table
333 III, larger group: 2.8 ± 2.3/h, smaller group: 3.0 ± 2.5/h; likelihood ratio test: $df = 1$,
334 $\chi^2 = 1.08$, $p = 0.30$).

335

336 *Patch Use*

337 The number of co-feeding individuals was larger in the larger group than in the smaller

group, although patch residency time, patch size, and inter-patch distance did not differ between the two groups (Table III; patch residency time: larger group: 407.3 ± 544.5 sec., smaller group: 350.7 ± 520.0 sec.; likelihood ratio test: $df = 1$, $\chi^2 = 0.07$, $p = 0.79$; patch size: larger group: 148.3 ± 211.1 m^3, smaller group: 137.6 ± 214.8 m^3; likelihood ratio test: $df = 1$, $\chi^2 = 3.58$, $p = 0.06$; number of co-feeding individuals: larger group: 0.91 ± 1.68 individuals, smaller group: 0.40 ± 0.99 individuals; GLMM: Estimate ± SE = -0.62 ± 0.10, $z = -6.48$, $p < 0.001$; inter-patch distance: larger group: 25.6 ± 33.0 m, smaller group: 28.3 ± 35.0 m; Wilcoxon rank-sum test: $W = 17791$, $p = 0.25$).

Both patch depletion and funneling, the assumptions of the ecological constraints model, did not occur more frequently in the larger group. First, we find neither significant difference in feeding rate between the two groups nor significant correlation between feeding rate and patch residency time for each group for all of the 12 main feeding items (Appendix II). Second, the proportions of filled patches among all visited patches did not differ between the two groups (larger group: 23/494, smaller group: 23/362; Fisher's exact test: $p = 0.29$). Contrary to the prediction, patch residency time was longer in the filled patches than in the non-filled patches in both of the two groups (Table IV, likelihood ratio test: larger group: $df = 1$, $\chi^2 = 50.19$, $p < 0.001$; smaller group: $df = 1$, $\chi^2 = 52.20$, $p < 0.001$). We also checked the following definitions of the number of feeding sites in a patch: (1) dividing an elliptic cylinder by 113 m^3 (the volume of a sphere with a radius of 3 m), (2) dividing an ellipsoid ((4/3)*major axis*minor axis*crown length*π) by 4.18 m^3, and (3) dividing an ellipsoid by 113 m^3. Since we were able to obtain the same results based on all of these definitions, only the results based on the initial definition are shown.

DISCUSSION

363 *Consistency with the Ecological Constraints Model*

364 In the present study, the larger group had a larger home range and spent more time
365 feeding than did the smaller group, in accordance with the predictions of the ecological
366 constraints model and the results of previous studies [Chapman & Chapman, 2000;
367 Majolo et al., 2009; etc.]. This suggests that intragroup scramble competition was more
368 intense in the larger group than in the smaller group.

369 To mitigate the costs of intragroup scramble competition, macaques in the
370 larger group changed dietary composition but did not increase dietary diversity. The
371 larger group spent more time feeding on mature leaves. Mature leaves are less
372 contestable because they are more abundant and less preferred than fruits / seeds and
373 young leaves [Agetsuma, 1995; Harris & Chapman, 2007; Hanya, 2009]. Among
374 Thomas's langurs (*Presbytis thomasi*), larger groups are also known to increase feeding
375 on less-preferred foods [Steenbeek & van Schaik, 2001]. In terms of patch use,
376 mature-leaf feeding positively influenced the number of co-feeding individuals (shown
377 in the model in Table III). Less-contestable foods enable animals to remain with many
378 individuals in a patch [Iwamoto, 1982; Agetsuma, 1995; Hanya, 2009]. Therefore, the
379 mature-leaf feeding might lead to maintaining spatial cohesion as a group. In addition,
380 the larger group spent more time feeding on fallen fruits / seeds and foraging (searching
381 for food in forest litter). Such terrestrial feeding might prolong the total feeding time in
382 the larger group, considering that there were no group differences in residency time on
383 the patch (tree or liana). Animals could save energy by increasing foraging on the
384 ground, given that terrestrial travel was less energetically costly than arboreal travel
385 [Janson, 1988; Hirsch et al., 2013]. In addition, dietary diversity did not differ between
386 the two groups. This contradicted the previous study, which suggested that larger groups
387 increased dietary diversity to deal with intense intragroup scramble competition

388 [Gogarten et al., 2014]. It is necessary to investigate energetic / nutritional intake of
389 animals in order to clarify whether this dietary strategy influences the fitness of animals.
390
391 *Inconsistency with the Ecological Constraints Model: Number of Visited Patches and*
392 *Patch Use*
393 One of the discrepancies between the results of our study and the ecological constraints
394 model is related to the number of visited patches and patch use. The ecological
395 constraints model predicted that larger groups stayed for shorter duration in one patch
396 and visited a larger number of patches [Chapman & Chapman, 2000]; however, patch
397 residency time and the number of visited patches were not different between the two
398 groups in the present study. There are two possible explanations for this.
399 First, patch depletion did not occur more frequently in the larger group. In our
400 study, we found no difference in feeding rate between the two groups and no correlation
401 between feeding rate and patch residency time for each group for all of the main feeding
402 items. This was consistent with previous studies demonstrating that increasing the
403 number of co-feeding individuals did not decrease feeding rate and that patch depletion
404 did not occur [Kazahari & Agetsuma, 2008; Tombak et al., 2012]. Furthermore,
405 Kazahari et al. [2013] demonstrated that the characteristics of the food items were
406 associated with the relationships between feeding-group size and feeding rate. For
407 example, feeding rate increased with feeding-group size in a patch where within-patch
408 food density was high. In our study, considering that the larger group depended more on
409 mature leaves, patch depletion will be unlikely to occur in the larger group because
410 mature leaves are superabundant within a patch. Thorough examination on the
411 time-series variations in feeding rate in combination with the characteristics of the food
412 items are required to elucidate this mechanism further in the Japanese macaques of

413 Yakushima.

414 Second, funneling did not occur in both of the two groups. The proportions of
415 filled patches did not differ between the two groups although it varied according to the
416 definitions (larger group: 4.7%–83.8%, smaller group: 6.4%–86.1%). Furthermore, in
417 contrast to the prediction, filling in patches did not shorten but prolonged patch
418 residency time. This could be explained by the result of a previous study that the
419 number of co-feeding individuals positively affected patch residency time in Japanese
420 macaques of Kinkazan Island [Kazahari & Agetsuma, 2008]. By staying with many
421 group members, macaques can be less dependent on following the group movement and
422 visually monitoring group members to maintain spatial cohesion [Kazahari & Agetsuma,
423 2010; Kazahari, 2014]. These results of funneling effect were robust regardless of the
424 definitions of feeding sites. Therefore, it is unlikely that feeding space in a patch
425 constrains patch residency time in Japanese macaques in Yakushima. Whether funneling
426 works as the mechanism of increasing the number of patches will depend on the
427 cost-benefit balance of group foraging, determined by the combinations of habitat
428 environment (patch size, presence of neighboring groups, etc.) and group size of a
429 population or species.

430

431 *Inconsistency with the Ecological Constraints Model: Travel Behavior*

432 The other discrepancy was travel behavior. In the present study, the smaller group
433 traveled longer distances and spent more time moving than did the larger group,
434 contrary to the predictions of the ecological constraints model. The intergroup
435 differences in travel distance and moving time were detected in our study even if other
436 factors such as dietary composition and mating behavior were controlled. There are two
437 possibilities to explain this. First, patch characteristics such as patch size, density, and

distribution could influence the moving behavior of animals [Maruhashi et al., 1998; Cords, 2012; Dunn et al., 2012]. When the relative group size was related to intergroup dominance, smaller-sized, subordinate groups may be obliged to use lower-quality home range than larger-sized, dominant groups [Cheney & Seyfarth, 1987; Harris, 2006; Scarry, 2013]. In this case, smaller groups are expected to travel longer distances in order to find high-quality food resources that have not been used by larger groups [Robinson, 1988; Koenig, 2002]. In our study, we controlled vegetation differences in the home ranges by selecting two neighboring groups as subjects. The two groups had partly overlapped home ranges in the same altitudinal zones, and inter-patch distance and patch size were not different between the two groups. Therefore, it is unlikely that the heterogeneity of vegetation causes the differences in moving behavior between the two groups.

Second, disadvantages in intergroup encounters could lead to great travel costs of subordinate groups. After losing intergroup encounters, defeated groups were forced to travel longer distances for a longer time than victorious groups [Srikosamatara, 1987; Crofoot, 2013]. In addition, defeated groups were forced to change travel direction, which may cause inefficient and extended travel routes [Srikosamatara, 1987]. The frequency of intergroup encounters in the Yakushima coastal forest was as high (0.067 times/h: smaller group in this study; 0.039 times/h: [Sugiura et al., 2000]) as those in the study sites of the previous studies which showed losing encounters led to longer travel distances (0.033 times/h [Crofoot, 2007; 2013]; 0.086 times/h [Srikosamatara, 1987], given that the observation time during daytime was 10 h per day). Considering that the intergroup encounters were aggressive in all of the study sites, the immediate consequences of the loss of intergroup encounters could accumulate as daily travel costs in the smaller group in Yakushima.

463 The results of our study on travel behavior also differed from those of Majolo
464 et al. [2009], which indicated that the larger group traveled longer distances and spent
465 more time moving, among Japanese macaques in the Yakushima coastal forest. This
466 would be explained by the difference in the relative and absolute sizes of the subject
467 groups. First, the size of the smaller group (18) in Majolo et al. was similar to the
468 average size of the neighboring groups (17.6), while the size of the smaller group in our
469 study (13–15) was half the average size of the neighboring groups (32.1). Under the
470 circumstance in Majolo et al., the smaller group might not be required to travel long
471 distances and/or for a long time as a consequence of losing encounters. Second,
472 Takahata et al. [1998] demonstrated that birth rate decreased further when group size
473 was less than 14 in the Yakushima coastal forest. The size of the smaller group (18) in
474 Majolo et al. was larger than that of the smaller group (13–15) in our study and that of
475 the group (14) that actually showed the lower birth rate in Takahata et al. Therefore,
476 only when the group size was below that threshold value and was smaller than the sizes
477 of the neighboring groups, animals in the group would have increased travel costs as a
478 result of intergroup competition.
479
480 *Implications of Population Dynamics in the Yakushima Coastal Forest*
481 This study revealed how feeding competition works in Japanese macaques in the
482 Yakushima coastal forest, which helps in understanding the behavioral mechanisms
483 underlying positive correlation between group size and reproductive success. Unlike
484 most primate species, birth rate increases with group size in the Yakushima coastal
485 forest. Previous studies in this population [Suzuki et al., 1998; Takahata et al., 1998]
486 have focused on the benefits of larger groups and costs of smaller groups through
487 intergroup contest competition from the point of view of energy intake: larger-sized,

dominant groups have higher-quality home ranges, which brings adult females better energetic / nutritional conditions and higher birth rate. Although intragroup scramble competition has not been investigated extensively, our study showed that the larger group had the costs of intragroup scramble competition, as has been reported in many of other primate species [e.g., Majolo et al., 2008]. In addition, our results were unique in proposing behavioral mechanism causing positive correlation between group size and reproductive success and suggesting that smaller groups have the costs of intergroup contest competition from the point of view of energy expenditure: smaller-sized, subordinate groups are required to travel long distances and/or for a long time, which worsens energetic / nutritional conditions of adult females and lowers birth rate. Travel behavior is energetically costly [Tucker, 1970; Dunn et al., 2013] and could affect energy balance, and in turn, reproductive success of adult females [Emery Thompson et al., 2012; McCabe et al., 2013]. To test how the costs and benefits of each group translate into the differences in reproductive success, the energy balance of the animals must be quantified: not only energy intake but also energy expenditure of animals in different-sized groups should be considered to understand the mechanisms of group-size effects on feeding behavior and reproductive success.

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662 **FIGURE LEGENDS**

663 Figure 1. Home ranges of the larger and smaller groups (scale: 1/25,000). Doubled lines

664 indicate a road running through the study area.

Table I. Summary of Variables in the GLMMs

Response variable	Unit of analysis	Explanatory variable	Error distribution	Offset term
Diet composition	Day	Group	Binomial	-
		Observation date (random)		
Activity budget	Day	Group	Binomial	-
		Copulation		
		Fruits / seeds feeding time		
		Animal matter feeding time		
		Observation date (random)		
Travel distance	Hour	Group	Gaussian	Observation time
		Copulation		
		Fruits / seeds feeding time		
		Animal matter feeding time		
		Animal ID (random)		
Number of visited patches	Hour	Group	Poisson	Feeding and moving times
		Copulation		
		Fruits / seeds feeding time		
		Animal matter feeding time		
		Animal ID (random)		
Patch residency time	Patch	Group	Gaussian	-
		Patch size		
		Number of co-feeding individuals		
		Food category		
		Animal ID (random)		
Patch size	Patch	Group	Gaussian	-
		Food category		
		Animal ID (random)		
Number of co-feeding individuals	Patch	Group	Zero-inflated Poisson	-
		Patch size		
		Food category		
		Animal ID (random)		
Patch residency time	Patch	Filled patch or not	Gaussian	Patch size
		Dominance rank		
		Food category		
		Animal ID (random)		

665

666

Tabel II. Summary of Activity Budget and Dietary Composition of the Larger and Smaller Groups

Activity	Diet	Larger group	Smaller group	Statistics
Feeding		45.1 ± 13.4	37.9 ± 14.0	$df = 1, \chi^2 = 9.13, p < 0.01$
	Fruits / seeds	37.2 ± 31.1	47.4 ± 38.3	$df = 1, \chi^2 = 2102, p < 0.001$
	Mature leaves	20.3 ± 23.0	16.7 ± 24.0	$df = 1, \chi^2 = 209.54, p < 0.001$
	Young leaves[a]	10.6 ± 20.2	14.6 ± 25.9	$df = 1, \chi^2 = 2668, p < 0.001$
	Flowers	1.5 ± 6.1	1.5 ± 4.5	$df = 1, \chi^2 = 0.0012, p = 0.97$
	Animal matter	1.0 ± 3.5	0.4 ± 1.9	$df = 1, \chi^2 = 0.13, p = 0.13$
	Fungi	0.3 ± 0.9	1.2 ± 3.8	$df = 1, \chi^2 = 0.20, p = 0.65$
	Other	3.2 ± 6.9	1.8 ± 4.2	-
	Unidentified	5.5 ± 7.7	5.7 ± 8.9	-
	Foraging	20.5 ± 17.9	10.5 ± 13.4	$df = 1, \chi^2 = 864.14, p < 0.001$
Moving		16.4 ± 4.8	22.0 ± 6.0	$df = 1, \chi^2 = 22.96, p < 0.001$
Resting		19.2 ± 9.6	16.3 ± 9.4	-
Grooming		19.2 ± 10.8	23.6 ± 14.2	-
Other		0.1 ± 0.3	0.2 ± 0.5	-

Mean percentage of time spent for each activity in a day ± SD is shown.

a, the result of the likelihood ratio test for GLM is shown.

667

Table III. Best-fit Models for Dietary Composition, Activity Budget, Number of Visited Patches, Travel Distance, and Patch Use

Item	Response variable	Explanatory variable	Estimate	SE	z	P
Dietary composition	Fruits / seeds	(Intercept)	-1.50	0.29	-5.19	< 0.001
		Group_Smaller	1.28	0.03	43.52	< 0.001
	Mature leaves	(Intercept)	-2.74	0.48	-5.76	< 0.001
		Group_Smaller	-2.01	0.16	-12.28	< 0.001
	Young leaves[a]	(Intercept)	-1.88	0.01	-354.62	< 0.001
		Group_Smaller	0.42	0.01	51.97	< 0.001
	Flowers	(Intercept)	-14.16	1.40	-10.09	< 0.001
	Animal matter	(Intercept)	-8.67	0.41	-20.95	< 0.001
	Fungi	(Intercept)	-15.22	1.83	-8.31	< 0.001
	Foraging	(Intercept)	-1.95	0.19	-10.31	< 0.001
		Group_Smaller	-0.91	0.03	-29.65	< 0.001
	Fallen fruits / seeds	(Intercept)	-4.74	0.45	-10.49	< 0.001
		Group_Smaller	-0.72	0.10	7.42	< 0.001
Activity budget	Feeding time	(Intercept)	0.10	0.11	0.95	0.34
		Group_Smaller	-0.31	0.10	-3.03	0.002
		Copulation	-0.03	0.11	-0.32	0.75
		Fruits / seeds feeding	-0.007	0.002	-3.59	< 0.001
		Animal matter feeding	-0.03	0.02	-1.36	0.17
	Moving time	(Intercept)	-1.64	0.07	-22.23	< 0.001
		Group_Smaller	0.38	0.08	4.98	< 0.001
		Copulation	-0.08	0.08	-0.91	0.37
		Fruits / seeds feeding	-0.0004	0.001	-0.30	0.77
		Animal matter feeding	-0.01	0.01	-0.80	0.42
Number of visited patches	Number of visited patches	(Intercept)	-2.79	0.06	-45.34	< 0.001
		Copulation	-0.05	0.16	-0.29	0.77
		Fruits / seeds feeding	0.0047	0.0009	5.31	< 0.001
		Animal matter feeding	-0.01	0.01	-1.59	0.11
Number of co-feeding individuals	Number of co-feeding individuals	(Intercept)	0.36	0.15	2.46	0.01
		Group_Smaller	-0.61	0.22	-2.76	0.006
		Patch size	0.001	0.0001	10.21	< 0.001
		Food category_mature leaves	0.24	0.11	2.23	0.03
		Food category_young leaves	0.07	0.13	0.55	0.58
		Food category_other	-0.46	0.22	-2.1	0.04

Item	Response variable	Explanatory variable	Estimate	SE	t
Travel distance	Travel distance	(Intercept)	9.18	0.30	30.40
		Group_Smaller	1.06	0.40	2.65
		Copulation	-0.14	0.81	-0.18
		Fruits / seeds feeding	0.01	0.01	1.86
		Animal matter feeding	0.06	0.03	1.74
Patch residency time	Patch residency time	(Intercept)	4.80	0.07	70.60
		Patch size	0.00	0.00	6.18
		Number of co-feeding individuals	0.26	0.03	8.27
		Food category_mature leaves	0.29	0.10	2.75
		Food category_young leaves	0.29	0.12	2.44
		Food category_other	-0.26	0.14	-1.85
Patch size	Patch size	(Intercept)	4.14	0.10	42.65
		Food category_mature leaves	-0.52	0.12	-4.34
		Food category_young leaves	0.55	0.14	4.06
		Food category_other	0.17	0.16	1.05

a, the result of GLM is shown.

Table IV. Best-fit Models for Funneling			
a. Larger group	Estimate	SE	t
(Intercept)	1.24	0.21	5.91
Filled_yes	2.12	0.29	7.21
Dominance rank	-0.42	0.30	-1.39
Food category_mature leaves	0.64	0.15	4.21
Food category_young leaves	-0.16	0.20	-0.80
Food category_other	-0.60	0.21	-2.87
b. Smaller group	Estimate	SE	t
(Intercept)	0.92	0.30	3.10
Filled_yes	2.07	0.28	7.46
Dominance rank	0.10	0.43	3.88
Food category_mature leaves	0.78	0.20	-1.61
Food category_young leaves	0.08	0.18	0.45
Food category_other	-0.42	0.26	0.23

Appendix I. Food Repertoire of the Larger and Smaller Groups

% to the total feeding time in the larger group	% to the total feeding time in the smaller group	Family	Species	Life Form	Part	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
5.15	5.49	Lauraceae	*Cinnamomum camphora*	Tree	Bud					L / S	L / S	L / S
2.50	3.66	Anacardiaceae	*Rhus succedanea*	Tree	Fruit	L / S	L / S	L / S				
1.75	3.66	Rubiaceae	*Psychotria serpens*	Liana	Mature leaf					L / S	L / S	L / S
2.28	3.63	Moraceae	*Ficus erecta*	Tree	Fruit		L / S	L / S		L / S	L / S	L / S
2.73	3.51	Lauraceae	*Litsea acuminata*	Tree	Fruit		L	L / S	L	L	L / S	
7.29	3.26	Rutaceae	*Zanthoxylum ailanthoides*	Tree	Seed	L	L / S	L / S				
1.43	3.04	Rubiaceae	*Morinda umbellata*	Liana	Fruit		L / S	L / S				
2.14	2.95	Moraceae	*Ficus wightiana*	Liana	Fruit	L / S	L		S	L		L
0.55	2.89	Fagaceae	*Lithocarpus edulis*	Tree	Fruit	L / S	L / S	L / S				
6.21	2.57	Moraceae	*Ficus wightiana*	Liana	Mature leaf			L	L / S	L / S	L	
3.62	2.37	Daphniphyllaceae	*Daphniphyllum teijimannii*	Tree	Mature leaf		L	L / S	L / S	L / S	L / S	L / S
1.54	2.35	Lauraceae	*Machilus thunbergii*	Tree	Shoot					L / S	L / S	L / S
1.51	2.19	Rubiaceae	*Morinda umbellata*	Liana	Mature leaf				L / S		L	
0.11	1.95	Theaceae	*Camellia japonica*	Tree	Nectar				L / S	L / S	L / S	L / S
2.78	1.92	Symplocaceae	*Symplocos lucida*	Tree	Mature leaf		L / S	L / S	L / S	L / S	L / S	L / S
3.51	1.66	Theaceae	*Eurya japonica*	Tree	Mature leaf				L	L	L / S	L / S
1.35	1.61	Theaceae	*Eurya emarginata*	Tree	Mature leaf	S				L / S	L / S	L
0.83	1.39	Rubiaceae	*Psychotria serpens*	Liana	Fruit	S	S	L	L / S	L		
0.49	1.29	Anacardiaceae	*Rhus succedanea*	Tree	Young leaf							L / S
0.67	1.27	Actinidaceae	*Actinidia rufa*	Liana	Fruit	L / S	L / S					
0.23	1.26	Fagaceae	*Quercus phillyraeoides*	Tree	Fruit	L / S	L / S	S				
1.73	1.25	Lauraceae	*Cinnamomum camphora*	Tree	Young leaf						L / S	L
1.45	1.23	Anacardiaceae	*Rhus succedanea*	Tree	Shoot							L / S
0.34	1.21	Myrsinaceae	*Ardisia sieboldii*	Tree	Fruit	S	L / S	S				
0.92	1.12	Aquifoliaceae	*Ilex integra*	Tree	Young leaf							L / S
0.36	1.01	Loranthaceae	*Taxillus yadoriki*	Liana	Fruit					S	L / S	S
1.57	0.95	Caprifoliaceae	*Lonicera affinis*	Liana	Shoot					L / S	L / S	L / S
1.90	0.85	Lauraceae	*Neolitsea sericea*	Tree	Fruit	L / S	L / S	L / S				
0.26	0.83	Moraceae	*Ficus pumila*	Liana	Fruit	L	L / S	S				
0.26	0.75	Sterculiaceae	*Firmiana plantanifolia*	Tree	Shoot							L / S
0.29	0.28	Capparidaceae	*Crateava religiosa*	Tree	Mature leaf						L	L / S
0.68	0.27	Moraceae	*Ficus erecta*	Tree	Mature leaf		L / S	L / S				L
0.17	0.25	Caprifoliaceae	*Lonicera affinis*	Liana	Young leaf					L / S	L	
0.20	0.19	Caprifoliaceae	*Lonicera affinis*	Liana	Fruit	L / S	L / S					
0.27	0.19	Ericaceae	*Vaccinium bracteatum*	Tree	Fruit	L / S	L / S					
0.72	0.18	Theaceae	*Eurya japonica*	Tree	Fruit	L / S	L / S	L				
1.69	0.17	Lauraceae	*Cinnamomum camphora*	Tree	Fruit	L / S						
0.48	0.16	Theaceae	*Camellia japonica*	Tree	Mature leaf		L		L / S			
0.27	0.15	Araliaceae	*Schefflera octophylla*	Tree	Mature leaf				L / S	L	L	
0.33	0.13	Capparidaceae	*Crateava religiosa*	Tree	Young leaf					L	L / S	
3.17	0.13	Meliaceae	*Melia azendarach*	Tree	Seed			L	L / S	L / S	L	L / S
0.53	0.11	Fagaceae	*Quercus salicina*	Tree	Fruit		L / S					
2.03	0.00	Anacardiaceae	*Rhus succedanea*	Tree	Stalk			L	L	L	L	
1.24	0.00	Symplocaceae	*Symplocos prunifolia*	Tree	Fruit	L	L	L				
0.95	0.00	Lauraceae	*Neolitsea sericea*	Tree	Flower			L				
0.76	0.00	Proteaceae	*Helicia cochinchinensis*	Tree	Fruit		L	L	L	L	L	
0.62	0.00	Caprifoliaceae	*Lonicera affinis*	Liana	Mature leaf				L			
0.61	0.00	Moraceae	*Ficus erecta*	Tree	Stalk			L	L	L		
0.48	0.00	Moraceae	*Ficus wightiana*	Liana	Shoot							L
0.35	0.00	Aquifoliaceae	*Ilex rotunda*	Tree	Bud						L	
0.33	0.00	Fagaceae	*Quercus phillyraeoides*	Tree	Flower							L
0.21	0.00	Symplocaceae	*Symplocos prunifolia*	Tree	Mature leaf				L	L		
0.20	0.00	Euphorbiaceae	*Glochidion obovatum*	Tree	Fruit		L					
0.19	0.00	Polypodiaceae	*Pyrrosia lingua*	Epiphyte	Mature leaf				L	L		
0.19	0.00	Fagaceae	*Quercus salicina*	Tree	Mature leaf				L			
0.15	0.00	Moraceae	*Ficus microcarpa*	Liana	Fruit					L		
0.14	0.00	Aceraceae	*Acer morifolium*	Tree	Flower bud						L	
0.13	0.00	Rubiaceae	*Psychotria rubra*	Tree	Fruit		L	L				
0.12	0.00	Proteaceae	*Helicia cochinchinensis*	Tree	Mature leaf					L	L	
0.00	2.41	Fagaceae	*Lithocarpus edulis*	Tree	Bud							S
0.00	1.09	Hamamelidaceae	*Distylium racemosum*	Tree	Gall							S
0.00	1.08	Euphorbiaceae	*Glochidion obovatum*	Tree	Young leaf						S	
0.00	1.06	Convolvulaceae	*Erycibe henryi*	Liana	Mature leaf				S			
0.00	1.06	Lauraceae	*Machilus thunbergii*	Tree	Fruit							S
0.00	1.05	Theaceae	*Ternstroemia gymnanthera*	Tree	Fruit	S	S	S	S	S		
0.00	0.88	Ebenaceae	*Diospyros japonica*	Tree	Fruit		S					
0.00	0.83	Vitaceae	*Parthenocissus tricuspidata*	Liana	Fruit	S						
0.00	0.70	Moraceae	*Ficus wightiana*	Liana	Young leaf							S
0.00	0.57	Anacardiaceae	*Rhus succedanea*	Tree	Mature leaf			S				
0.00	0.55	Rubiaceae	*Morinda umbellata*	Liana	Young leaf							S
0.00	0.52	Lauraceae	*Litsea acuminata*	Tree	Mature leaf					S	S	
0.00	0.50	Fagaceae	*Lithocarpus edulis*	Tree	Bark						S	
0.00	0.41	Aquifoliaceae	*Ilex integra*	Tree	Bud							S
0.00	0.38	Asteraceae	*Farfugium japonicum*	Herb	Mature leaf					S	S	
0.00	0.27	Gleicheniaceae	*Dicranopteris linearis*	Fern	Mature leaf					S		
0.00	0.23	Chloranthaceae	*Sarcandra glabra*	Herb	Pith					S		S
0.00	0.22	Asteraceae	*Cirsium spinosum*	Herb	Mature leaf					S		
0.00	0.21	Lauraceae	*Litsea japonica*	Tree	Fruit					S	S	
0.00	0.18	Vervenaceae	*Callicarpa dichotoma*	Tree	Fruit		S					
0.00	0.17	Moraceae	*Ficus erecta*	Tree	Bud					S		
0.00	0.14	Moraceae	*Ficus nipponica*	Liana	Fruit	S						
0.00	0.13	Theaceae	*Camellia japonica*	Tree	Fruit							S
0.00	0.12	Myrsinaceae	*Maesa tenera*	Tree	Mature leaf			S				
0.00	0.11	Primulaceae	*Lysimachia sikokiana*	Herb	Mature leaf						S	S

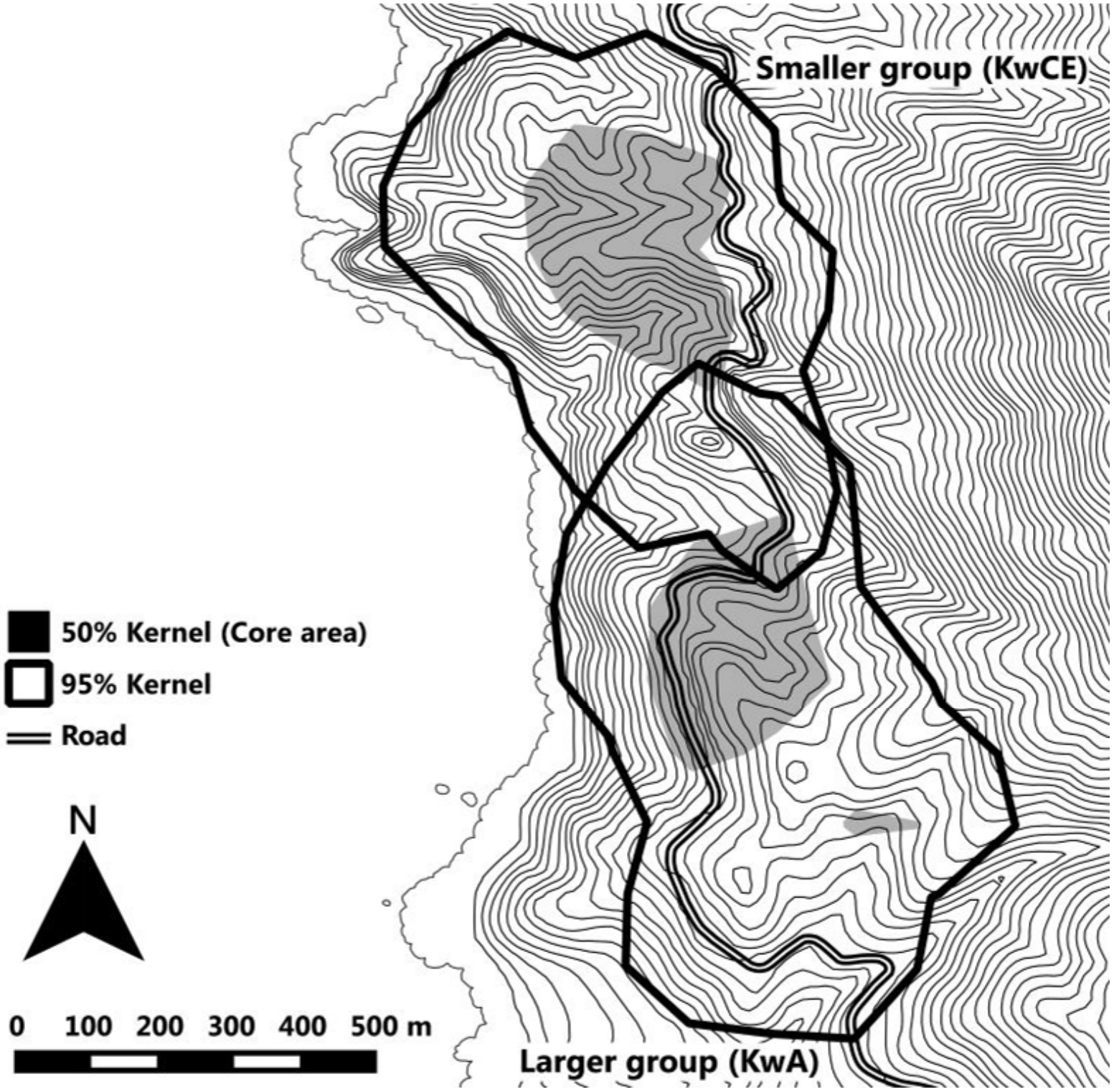
L / S indicates that the food was eaten by the larger and smaller groups in the month.
L, Larger group; S, Smaller group.

Appendix II. Comparison of Feeding Rate between the Larger and Smaller Groups and Correlation between Feeding Rate and Patch Residency Time in the Two Group

Species	Part	Feeding rate (unit/sec.)		Wilcoxon rank-sum test	Correlation with patch residency time[a]	
		Larger group	Smaller group		Larger group	Smaller group
Ficus wightiana	Fruit	0.48 ± 0.56	0.55 ± 0.16	$p = 0.7$	$p = 0.13$	$p = 0.75$
Litsea acuminata	Fruit	0.33 ± 0.16	0.29 ± 0.10	$p = 0.14$	$p = 0.09$	$p = 0.50$
Rhus succedanea	Fruit	0.51 ± 0.17	0.38 ± 0.12	$p = 0.06$	$p = 0.07$	$p = 1$
Rhus succedanea	Young leaf	0.30 ± 0.19	0.25 ± 0.23	$p = 0.3$	$p = 0.78$	$p = 0.33$
Daphniphyllum teijimannii	Mature leaf	0.13 ± 0.14	0.12 ± 0.05	$p = 0.38$	$p = 0.23$	$p = 0.33$
Ficus erecta	Fruit	0.36 ± 0.27	0.43 ± 0.27	$p = 0.36$	$p = 0.89$	$p = 0.24$
Zanthoxylum ailanthoides	Fruit	0.70 ± 0.21	0.72 ± 0.17	$p = 0.97$	$p = 0.59$	$p = 0.10$
Symplocos lucida	Mature leaf	0.17 ± 0.07	0.23 ± 0.14	$p = 0.35$	$p = 0.55$	$p = 0.95$
Cinnamomum japonicum	Young leaf	0.48 ± 0.10	0.49 ± 0.08	$p = 0.92$	$p = 0.17$	$p = 1$
Lithocarpus (Pasania) edulis	Fruit	0.16 ± 0.04	0.23 ± 0.15	$p = 0.63$	$p = 0.33$	$p = 0.92$
Neolitsea sericea	Fruit	0.77 ± 0.28	0.66 ± 0.10	$p = 0.31$	$p = 0.50$	$p = 1$
Machilus thunbergii	Shoot	0.26 ± 0.17	0.32 ± 0.23	$p = 0.58$	$p = 0.33$	$p = 0.92$

a, the results of Spearman's rank order correlation test are shown.

Figure 1


Smaller group (KwCE)
50% Kernel (Core area)
95% Kernel
Road
N
0 100 200 300 400 500 m
Larger group (KwA)